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THE MUTANT CROSSVEINLESS IN DROSOPHILA MELANOGASTER*

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The Origin of Crossveinless.—A recessive sex-linked mutant called small-eye appeared, the locus of which was found to be very close to that of fused (locus of *fu*, 59.5). To determine definitely the relation of the two loci, a forked (locus of *f*, 56.5) small-eye (symbol, *sy*) female was crossed to a fused male, and five of the F_1 wild-type females were mated singly to forked small-eye brothers. In F_2, no crossovers between small-eye and fused were obtained. While this result confirms the closeness of the loci, it was decided to raise more F_2 cultures until one or more cross-overs appeared which would show the position of the new locus with reference to the known loci forked and fused. Accordingly, from one of the five F_2 cultures (No. 10,846) four wild-type females, of the same constitution as the original F_1 female, were mated to forked small-eye brothers. There appeared two cross-overs (wild-type) that showed that the locus of small-eye is to the left of that of fused (and about 0.2 unit distant, i.e., at 59.3).

In one of these four cultures it was noticed (No. 10,988, Dec. 21, 1919) that about half the males did not have either anterior or posterior cross-veins. All females had normal crossveins. Evidently crossveinless (*cv*) is a sex-linked recessive. The other three sister cultures were then examined, and no crossveinless flies were present.

The males that hatched after the mutant character was noticed were: *cv f sy* 12, *fu* 11, *cv fu* 3, *f sy* 9. Since approximately half the males showed the crossveinless character, the mother is known to have been heterozygous for the mutant gene. The crossveinless character emerged in association with forked more often than with fused, which means that the mutant gene was in the forked small-eye chromosome of the mother. She had received this chromosome from her father—the F_1 forked small-eye male used in raising culture 10,846. But three of her sisters likewise received forked small-eye sperm from this same male, and, as we have seen, none of these three sisters received the crossveinless gene. It follows that the mutation occurred relatively late in the ontogeny of the testis of the male in question, perhaps as late as the maturation stage.

The Locus of Crossveinless.—Of the thirty-five males in which the linkage relations of crossveinless to forked, small-eye, and fused were noted, 12, or 34.3%, were crossovers between crossveinless and forked. In view of the small numbers, this value indicated only that the locus of crossveinless is to the left of that of forked and probably at least as distant as vermilion (*v* locus, 33.0). The next step was to mate a crossveinless forked small-eye male to a vermilion female and to raise several F_2 cultures (table 1).

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* Contribution from the Carnegie Institution of Washington.

TABLE 1

P_1, Crossveinless Forked Small-eye ♂ × Vermilion ♀; F_1 Wild-Type ♀, $\frac{cv \quad f \quad sy}{v}$ × F_1 Vermilion ♂ (Table Includes F_2 ♂ ♂ Only)

JAN. 20, 1920	0		1		2		3		1,2		1,3	
	cv f sy	*v*	*cv v*	*f sy*	*cv*	*v f sy*	*cv f*	*v sy*	*cv v f sy*	+	*cv v sy*	*f*
11223	64	60	19	15	22	17	3	1	1	1	–	–
11225	41	63	16	19	18	10	1	–	1	2	–	–
11226	42	52	16	14	25	14	2	2	1	2	1	–
11227	63	62	18	10	19	16	1	–	–	2	1	–
11268	102	84	29	24	39	31	1	1	4	4	–	–
11275	89	110	31	27	27	33	1	3	2	3	–	–
11276	10	22	3	4	5	8	–	1	–	2	–	1
Total.....	411	453	132	113	155	129	9	8	9	16	2	1

The locus of crossveinless, on the basis of the F_2 males, proved to be about 19.0 units to the left of vermilion, that is, about 14 units from the zero end of the chromosome. This location is regarded as especially valuable since the interval from ruby (7.5) to cut (20.0) did not contain any serviceable mutant character. The rather poor mutants club (16.7), lemon (17.5), shifted (17.8), and depressed (18.0) had all been lost or discarded. It was important to have a mutant of first rank in this region in order to investigate the linkage behavior of lethal-2, which is probably a "deficiency." A multiple stock, ruby cut tan (*t*, 27.5) vermilion had been made up for this analysis, and it was decided to incorporate the crossveinless character in the multiple. In the process of incorporating crossveinless, accurate knowledge of the location of crossveinless was obtained from the F_2 results of the cross between crossveinless male and females of the original multiple (table 2).

There was 8.5% of crossing over between ruby and crossveinless, and 8.3% between crossveinless and cut. The locus of crossveinless is thus almost exactly in the middle of the gap between ruby and cut. The total amount of crossing over between ruby and cut was 16.8 which is slightly higher than the expected value 12.5.

This position of crossveinless makes it possible to study linkage relations in any part of, or throughout the *X*-chromosome, by means of mutants so close together than no unobserved double crossing over occurs. Furthermore, these mutants are perfectly classifiable in combination, and, with the exception of cleft at the extreme right end of the chromo-

TABLE 2

P_1, CROSSVEINLESS ♂ × RUBY CUT TAN VERMILION ♀ ; F_1 WILD-TYPE ♀, $\frac{rb \quad ct\ t\ v}{cv}$, × F_1 *rb ct t v* ♂ (TABLE INCLUDES F_2 ♂ ♂ ONLY)

FEB. 14, 1920	0		1		2		3		4		1,3		1,4		2,3	2,4
	rb ct t v	*cv*	*rb cv*	*ct t v*	*rb*	*cv ct t v*	*rb ct*	*cv t v*	*rb ct t*	*cv v*	*rb cv t v*	*ct*	*rb cv v*	*ct t*	*rb t v*	*rb v*
11328	63	87	6	15	17	14	10	7	7	7	–	1	–	–	–	–
11329	62	74	12	6	8	7	7	5	8	5	1	2	3	1	1	1
11330	75	77	6	5	7	4	10	9	6	6	–	–	–	–	–	1
11331	86	74	15	4	8	5	9	9	7	7	–	–	–	–	–	–
11332	72	87	5	8	6	12	10	6	2	17	1	–	–	–	–	–
11333	75	77	10	8	10	7	10	6	10	6	1	–	–	–	–	–
11400	47	44	4	8	4	4	5	2	5	5	–	–	–	–	–	–
11418	59	70	10	5	9	8	5	8	3	2	–	–	1	–	1	–
Total.....	539	590	68	59	69	61	66	52	48	55	3	3	4	1	2	2

some, are of such excellent viability that they can be used simultaneously with only negligible differential mortality. Crossveinless is one of the best of these characters, since the somatic effect is so slight that interference with the classification of other mutants is at a minimum. It is a matter of observation that mutants like crossveinless with slight somatic effects are generally those with least disturbance to viability. A striking example of this correlation is to be found in the cut mutations. On at least eleven occasions sex-linked mutations that were similar to the original cut have appeared. Of these, cut^3 was both the poorest in viability and the most extreme in extent and number of somatic changes, while cut^6 was the best in viability and least extreme in its single observed somatic change. Two of the other allelomorphs, were intermediates in

TABLE 3

P_1, CROSSVEINLESS ♀ × CUT^6 ♂; F_1 WILD-TYPE ♀, $\frac{cv}{ct^6}$, × F_1 *cv* ♂ (F_2 ♂ ♂ ONLY)

APR. 14, '20	*cv*	ct^6	*cv* ct^6	+	CONT.	*cv*	ct^6	*cv* ct^6	+
11700	88	95	9	8	11733	228	235	15	14
11701	81	75	7	7	11734	143	164	11	12
11702	108	106	7	10	11735	89	88	6	7
11703	22	26	2	2	11736	135	156	7	12
11704	91	88	4	5					
					Total.....	985	1033	68	77

both these regards, while differing from each other. Cut^6 is now the only cut mutant used for linkage determinations involving this locus.

Additional linkage data upon the crossveinless cut distance was obtained by raising nine F_2 cultures from the cross of crossveinless to cut^6. The crossover value was found to be 6.7 on the basis of the 2,163 flies (table 3).

The locus of crossveinless is at 13.7, as calculated on the basis of the data of the three preceeding tables, and on the assumptions that the locus of ruby is at 7.5 of cut at 20.0, and of vermilion at 33.0.

Description of the Crossveinless Character; Homology with Crossveinless in D. virilis.—The somatic changes produced by the crossveinless gene seem to be restricted to the entire absence of the posterior crossvein and the almost complete absence of the anterior crossvein. There is a slight trace only of the anterior crossvein, though on casual inspection it seems to extend outward from the III-longitudinal vein about half way to the IVth. However, what is seen is largely a sense-organ that is normally present near the mid-point of the anterior crossvein and that is not affected by the crossveinless mutation. Examination of crossveinless in D. virilis showed that the sense organ is unaffected there also, but that the crossvein is not reduced in length or thickness as much as in D. melanogaster. (See figures of the crossveinless mutant in Weinstein's paper preceding this.)

The similarity of the characters is parallelled by a similarity of position on the maps of the two X-chromosomes. It seems highly probable that the two mutants are homologous, though, as Weinstein's discussion brings out, this cannot yet be accepted without reservations.

IS CROSSING OVER A FUNCTION OF DISTANCE?[1]

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There is a well intrenched concept of recent genetics that hereditary factors or genes may be given fairly definite loci on chromosome maps and that these maps correspond to or represent, roughly perhaps, the actual conditions in the chromosome. The basis for this attractive and suggestive view is the premise that the distance between two genes is necessarily proportional to the percentage of crossing over which these two genes show—other things being equal. If the distance which gives one per cent of crossovers is used as an arbitrary unit of measurement, then it follows that distances on the chromosome may be calculated in terms of this unit. It has seemed to me for some time that the antecedent in this hypothetical proposition contains a more or less gratuitous assumption.